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THE

BOTANICAL GAZETTE

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EXPERIMENTAL INVESTIGATIONS ON THE GENUS RAZOUMOFSKYA

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(WITH NINETEEN FIGURES)

Introduction

This article is the first of a series of reports on culture experiments of mistletoes. The work was begun in September 1911, and will be continued indefinitely. The aim of these experiments is to determine the validity of the several species as now distinguished, their affinities to each other, hosts on which they may be of economic importance or on which they may occasionally occur, and influence of host and condition of host as governed by its environment on the form, color, or other diagnostic characters commonly employed in the classification of these parasites. Since the systematic position and host relationships of several of these plants are not definitely defined, and since they are of great economic importance in many forest regions, it is believed the work will be of consider-The plan of these reports is to record as briefly as possible the results of each series of cultures as completed. The present report includes considerable discussion, owing to the necessity of outlining the problems in hand. The detailed discussion of results and technical description of species will be reserved until the conclusion of the experiments.

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Methods

For that part of the work being conducted at Missoula, Montana, the opportunities are very favorable. Practically all the species of Razoumofskya of any economic importance are of easy access from the laboratory. Members of the field force of the United States Forest Service are aiding in the work by sending in fresh mature specimens of R. pusilla on spruce and larch from the Lake states, and of the rare unclassified forms occurring on white and yellow pines in Oregon, Idaho, Utah, and Nevada. A great deal of material of the common forms from all parts of the Northwest has also been contributed. The writer visits regularly the various forests of the Northwest and has made abundant collections of the mistletoes of these regions. The writer is under particular obligations to Professor W. C. Weir for service in connection with cultures at Bellingham, Washington; to L. H. WEIR for collecting special material; to D. R. Brewster of the Forest Service Experiment Station, at Priest River, Idaho, and to J. Duncan, Superintendent of Parks of the city of Spokane, for permitting cultures to be made on various exotic conifers; and to E. E. HUBERT of this laboratory for assistance in making cultures.

From 1911 to 1914 inclusive the inoculations were conducted in the open. Seeds were sown on trial hosts of species other than that on which they developed, either in the same vicinity or in widely separate regions. In the latter case trial hosts of the same species as that on which the mistletoe grew were also included. This served to check the viability of the seed, also to bring out differences due to change of environment between the plants resulting from inoculation on the same host species and the plants furnishing the seed. The same was true for the plants on trial hosts other than that on which the parent plant developed. double procedure demanded copious notes on the conditions of growth and general morphology of the plants furnishing the seed used in inoculations in other regions and the saving of specimens of both sexes for comparison afterward. The same was done with plants resulting from inoculation. In the latter case, where necessary, the infected branch or stem was cut out to prevent the spread of the parasite in new regions. A large number of specimens are

accumulating, but this seemed desirable in case all necessary notes were not taken on both generations. In the case of continuing the inoculations of the same species of mistletoe through several generations on the same host but different individuals, either in the same or different localities, or on different host species, the saving of specimens fully recorded is doubly necessary. This should also furnish some information on the subject of the germinal transmission of characters.

Cultures begun in 1914 are being conducted both in the field and in the greenhouse. This doubles the amount of work, insuring greater dependency on results; and in the case of the indoor work closer study is possible of the life history of a successful inoculation. Indoor work also permits the use of a larger number of trial host species. The seeds germinate more rapidly and results are sooner obtained. One of the chief reasons for maintaining outdoor cultures is to check, whenever possible, under natural conditions, any unusual result obtained in the greenhouse. Cultures in the open have so far proved more successful than those inside, where the same mistletoes and hosts were concerned. If, however, a few unusual hosts are obtained indoors, it must be remembered that it is a new association of host and parasite often not possible in nature; moreover, some of the mistletoes showing the greatest predilection for a particular host or host genus are occasionally found on trees belonging to other genera.

In making the inoculations great care is exercised to attach the seeds at the most vulnerable points, such as in the axils of the leaf sheaths, tender branches, base of terminal buds, and in the denser zone of needles at the nodes. Observations show that infection usually occurs at these places. Before the seeds are transferred to the host they are allowed to stand for a few minutes in water. This causes the mucilaginous coat of the seed to expand. The seeds are then sucked against the point of a dropping pipette and placed firmly in the desired position. After a short time the mucilaginous layer dries, holding the point of the seed in place.

The host material used in the inoculations ranges from seedlings 2 years old to the tender branches of mature forest trees. In case

¹ Weir, James R., Wallrothiella Arceuthobii. Jour. Agric. Research 4:377. 1915.

of the trial host possessing a suberized cortex the seeds are sown only on the first to the sixth year's growth. It has already been demonstrated that infection will not normally take place on older tissues.2 It has been experimentally proven, however, that by scraping away the dead surface tissues of the bark on parts of branches as old as 7 years, and which still contain chlorophyll, it may be possible to secure infection. The number of seeds sown on each trial host has been maintained at 20 for greenhouse cultures and, owing to possible accident to the seed, 50 for outdoor work. It seemed desirable to try to maintain the seed at a fixed number so that the relative susceptibility of all trial hosts to any one form of mistletoe may be compared. Because it is impossible, especially of cultures in the open, to know that all seeds sown remained on the trees, the relative susceptibility of all trial hosts was further tested in most cases where it was particularly desirable to do so and whenever it was possible, by using a fixed number of trees of any one genus. A record of the source of seed of all trial hosts and of the place where the trees were grown was kept. This seemed desirable in view of the question of influence on the morphology of the parasite. In the case of transplants the trees had not been transplanted very long to the place where cultures were made. seeds demand a period of rest before germination, and if stored under cool and moist conditions may be carried over and sown in the spring. Sowings as late as April have resulted in successful inoculations. The low temperatures of winter also seem beneficial to the seed, as it is observed that a higher percentage of seeds germinate which have undergone freezing temperatures. probably accounts for the greater number of positive results obtained in outdoor cultures. If the seeds are stored in warm, dry air, they lose their vitality very rapidly, owing to the evaporation of moisture from the chlorophyllaceous endosperm. Germination tests show that the seeds are capable of germination some 2 weeks before they are normally expelled from the capsule, so that it has been possible to sow the seeds of some species early in September. Care must be taken in sowing seeds on Larix before

² Weir, J. R., Mistletoe injury to conifers in the Northwest. U.S. Dept. Agric. Bull. 360. p. 8. 1916.

the leaves have fallen; otherwise the seeds placed on the foliar spurs will be carried away with the falling leaves.

The cultures of the false mistletoes may be considered difficult. There must first be considerable knowledge of the requirements for seed germination, and of the plants afterward, in the case of the work done indoors. Much that is necessary has been learned, and the work is now going on more rapidly. The following is the first detailed report of the culture of mistletoes in this country. Some work of this kind



FIG. 1.—Razoumofskya campylopoda on Pinus ponderosa: slender, branching form with stems more or less cylindrical at base, pistillate; Oregon coast; reduced one-fourth.

but in another connection has already been reported by the writer (loc. cit.).

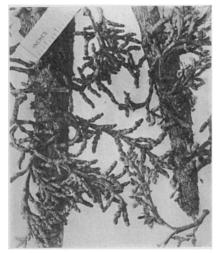


FIG. 2.—R. campylopoda on Pinus ponderosa: short, thick form with angular stems, staminate and pistillate plants; Oregon coast.

Cultures with yellow pine mistletoes

Razoumofskya campylopoda (Engelm.) Piper and R. cryptopoda (Engelm.) Coville, the largest and most conspicuous members of the genus in the United States, are supposedly 2 distinct species occurring on yellow pines. The former (figs. 1, 2, 6) is based on specimens from north Idaho or northeastern Washington, and is principally confined to the coast and northern Rocky

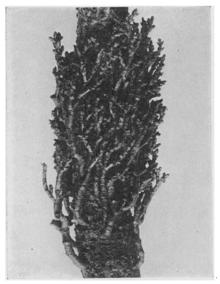


Fig. 3.—R. cryptopoda on Pinus ponderosa: pistillate; New Mexico; reduced one-fourth. —Photograph by G. G. HEDGCOCK.

flowers, and position of anthers on the calyx lobes, characters usually employed to distinguish one species from the other, are not always constant in these plants from the several regions in which they are supposed to occur, but apparently merge into one form or the other with change of habitat, just as is the case in any other species having a wide distribution and range of hosts. In a series of experiments recently completed by the writer and not otherwise mentioned in this paper it has

Mountain regions.³ The latter (figs. 3-5), based on specimens from New Mexico, is apparently limited to the southern Rocky Mountain regions. Both plants were originally described from specimens on Pinus ponderosa, which is their most common host. A large collection of these plants on P. ponderosa and a number of other hosts from their respective regions shows so few constant distinguishing characters by which the plants from the two geographical regions may readily be separated that it seemed desirable to test them out by cultures. Color, branching, thickness of stems, parting of



Fig. 4.—R. cryptopoda on Pinus ponderosa: staminate and pistillate; southern Utah.

³ PIPER, CHARLES V., Contrib. U.S. Nat. Herb. 11:222. 1906.

been demonstrated that size and color of flowers, stem, fruit, form and division of calyx lobes, slenderness and length of plant, com-

pactness of individual colonies of the northern form depend upon age of the plants and of the infection, nourishment, condition, location, and species of host. In view of these results it seems desirable that the diagnostic characters as now employed in the separation of the large plants on yellow pines should be substantiated by a large number of cultures before



FIG. 5.—R. cryptopoda on Pinus chihua-huana: pistillate; reduced one-half.—Photograph by G. G. Hedgcock.

they can be held specifically distinct. Experiments involving the transfer of seeds of the northern and coast plant from its various



FIG. 6.—R. campylopoda on Pinus ponderosa as it often appears growing from an advancing cortical stroma in branches of witches' brooms: plants pistillate, mature.

hosts to Rocky Mountain yellow pines, and vice versa, in their respective regions should be of some value in determining the validity of the two alleged species.

R. occidentalis abietina Engelm. (figs. 7, 8) is a large form of mistletoe found on Abies throughout California, Washington, Oregon, and Idaho. It closely resembles the large mistletoes on yellow pines and is described as a variety of the form R. campylopoda (figs. 1, 2, 6) (Arceuthobium occidentale). The plant is not so large as the

latter, but both have the same color variations and bloom and fruit in the same period. The facts that it is usually found in

the same regions where the yellow pine mistletoe occurs, has the



FIG. 7.—R. occidentalis abietina on Abies concolor: staminate and pistillate plants; Oregon.

same diseases attacking it, and is not found in regions where the typical R. tsugensis is most abundant and which it also slightly resembles, indicate that it may be a biological form of the former. The results of a number of cultures involving the three plants mentioned are presented in table I.

It will be seen from table I that an effort has been made to sow the seed of the large mistletoes on *Pinus ponderosa* (figs. 1-6) from several localities on as many different hosts as possible and on the same host in widely separate regions.

The object of the latter was to try to determine the relationship

of the common mistletoes with thick, robust stems on yellow pine in the Rocky Mountain region to the more slender form on the same host in the Pacific Coast region. This problem has been sufficiently outlined previously. The cultures so far do not furnish any evidence that the two forms should be considered identical. Plants in the Pacific

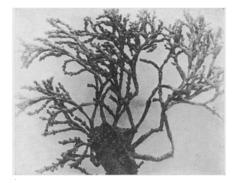


Fig. 8.—R. occidentalis abietina on Abies nobilis: staminate plants; Oregon.

Coast region resulting from seed collected in the northern Rocky Mountain region, and vice versa, exhibit various color varia-

tions, depending upon the region where grown. The same variation is noted in the robust form when grown in the North. shows that these plants from the different localities cannot be held specifically distinct on a basis of color. Although color has been one of the chief distinctions between the two, the cultures show that there is no marked difference in the general morphology of each form when grown outside of its original place of collection. True, there are some differences to be noted with respect to size, but it is purely a matter of age of infection. Even after the first maturity these plants, which have a comparatively long life, grow larger by developing additional branches and increasing the thickness of the stem. The comparisons made in the table are based on plants differing widely in age; consequently measurements must vary slightly. Excepting color changes, which were to be expected from varying habitats, the general morphology of the younger plants of the parent colonies were in no particular different from those of the cultures. The cultures have also demonstrated the fact that R. campylopoda will infect Abies, with considerable variation in color and size of the resultant plants, but closely resembling the form known as R. occidentalis abietina. It is interesting to note in this connection that COVILLE4 refers the plant found on Abies magnifica and A. concolor directly to R. campylopoda (R. occidentalis [Engelm.] Coville) with the statement that it is probably the plant that Engelmann⁵ had previously described under this name (Arceuthobium campylopodum). It is further shown that R. campylopoda will infect Picea and Larix, but with difficulty.

This mistletoe also will apparently readily infect *Pinus contorta*, a result repeatedly confirmed in the field. This tree, however, is not a common host. As will be shown in the case of *R. americana*, it is believed that this parasite may be expected to occur on any hard or yellow pine, but with predilection for certain species. The mere assumption that hosts are the determining factors of a species is here shown to be untenable. When a parasitic species will infect hosts from widely separate regions and even genera, and the resulting plants have certain characters varying from those exhibited

⁴ Contrib. U.S. Nat. Herb. 4:192. 1893.

⁵ GRAY, ASA, Pl. Lindh. 2:214. 1850.

TABLE I

FROM THE LARGE MISTLETOES ON Pinus ponderosa COMMONLY KNOWN IN THEIR RESPECTIVE REGIONS AS R. campylopoda and R. cryplopoda; cultures from seed collected in the Santa Barbara National Forest, California, marked A; cultures Seed collected September 25, 1911, St. Maries, Idaho; September 29, 1912, Santa Barbara National Forest, California; September 30, 1912, and at intervals from September 4 to November 14, 1914, at Spokane, Washington, and in Utah, From seed collected at St. Maries, Idaho, marked B_j cultures from seed collected in Utah marked C.

TRIAL HOSTS	OSTS		LOCALITY WHERE		RESULTS OF CULTURES
Name and number used in cultures	Source of seed	Locality	CULTURES WERE MADE AND DATE	Date of first observation of germination	Results (measurements averaged)
Pinus ponderosa (2) Local	Local	Local	Priest River, Idaho 10-6-12, A*	6-26-13	6-26-13 October 14, 1916: 1 infection on each host; all staminate (a) 3 cm. high, deep olive,‡ mature, flowering spikes 1 cm. long (no. 637); (b) 3 cm. high; general color, yellowish olive; nodes vinaceous brown (no. 638); parent, 6 cm. high; much branched, yellowish olive (no. 636).
Pinus ponderosa (2) Local	Local	Local	Priest River, Idaho 10-4-12, C*	5-10-13	October 15, 1016: I infection on each host, staminate and pistillate; former 3.5 cm. high, robust, thick at base; branches, somewhat paniculate, dark greenish olive; floral spikes I cm. long; flowers mostly 3-parted, compressed; latter 5 cm. high, stems thick at base, light brownish olive, mature; seed greenish olive, 3.02 by 1.44 mm.; parent, pistillate; stems light olive yellow, thick at base, robust throughout, 4 cm. high; fruit, olive yellow; seed, 3.04 by 1.45 mm.; staminate, olive yellow; branches, short, 4 cm. high; floral spikes, 1.5 cm. long; flowers, 3 and 4-parted.

, Wash. 4-10-12 September 19, 1915: 3 infections: (a) staminate, (b) staminate, (c) pistillate; all 5 cm. high. (a) Stems seal brown; floral spikes, light yellowish olive mature; 1 cm. long; flowers mostly 3-parted; exposed (no. 671). (b) Stems uniformly olive yellow; floral spikes 7 mm. long; flowers 3 and 4-parted; developed in shade (no. 672). (c) Olive yellow; fruiting spike darker; fruit vinaceous gray; seed 3.02 by 1.45 mm. (no. 673). Parent, pistillate, 6 cm. high; stems tawny olive; fruit pale green-blue gray; seed 3.0 by 1.3 mm. (no. 674); staminate \$\frac{8}{3}\$ ocm. high; and nostly 4-parted (no 675).	Mont. 5-10-13 October 1, 1916: 1 infection; pistillate, 6 cm. high, branched, uniformly light brownish olive; fruit not produced (no. 639); parent 5 cm. high, uniformly dark livid brown (no. 640).	iest River, Idaho, 6-19-13 October 15, 1916: 1 infection; pistillate, 2 cm. (Experiment Station) high, light yellowish olive (no. 641); parent tion) yellowish olive (no. 635).	(Experiment Stateminate and pistillate; former 3 cm. high, light olive, yellow floral spikes 1.5 cm., flowers nostly 3-parted (no. 632); latter 2.5 cm. high, yellowish olive, mature, seed 3.02 by 1.42 mm. (no. 631); parent pistillate; stems isabel, fruit russian blue, seed 3.1 by 1.53 mm. (no. 631); staminate, light brownish olive, much branched, 7 cm. high, floral spikes 2 cm. long, flowers 3 and 4-parted (no. 634).
nd Bellingham, Wash. Io-10-11, * B	Missoula, Mont.	Pr	Priest River, Idaho (Experiment Station) 10-4-12,* A
Cal. and Wash.	al Local	. Mont.	Ocolo.
Cal.	<u>Loc</u>	S.D.	Colo
Pinus ponderosa (2)	Pinus ponderosa (2) Local	Finus ponderosa (var. scopulorum) (2)	Pinus ponderosa (2)

CABLE I—Cont	inued
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RESULTS OF CULTURES	Results (measurements averaged)	October 15, 1916: 1 infection, pistillate, 2 cm. high, ecru-olive (no. 642); parent olive yellow, fruit russian blue (no. 643).	October 14, 1916: I infection, pistillate, 3 cm. high, buffy olive (no. 644); parent 8 cm. high, clay color (no. 645).	November 1, 1916: 1 infection, plants appearing; tree died on being transplanted into greenhouse.	October 14, 1916: I infection, staminate, 4 cm. high, dark greenish olive, floral spikes 1.5 cm. long, flowers 3 and 4-parted (no. 647); parent pistillate, 7 cm. high, olive-ocher, fruit yellowish olive (no. 648); staminate, 5 cm. high, honey yellow flowered, spikes I cm. high, flowers mostly 3-parted.	October 14, 1916: 2 infections on 2 different trees; plants pistillate, one 3.5 cm. high, purplish lilac at nodes, remainder of stem reed yellow, fruit not produced (no. 629); the other (no. 630) 2 cm. high, yellowish olive, fruit not produced; parent honey yellow, on same branch with deep yellow staminate plants (no. 628).	January 3, 1917: 2 infections; plants staminate, 3 cm. high, olive yellow (no. 646); parent yellowish olive (no. 649).	October 15, 1916: r infection, stammate, infected twig stunted, almost dead; one plant attached, remainder fallen, army brown (no. 650); parent light yellowish olive, fruit dark greenish olive (no. 651).
	Date of first observation of germination	6-19-13	6-26-13	4-28-15	6-26-13	6-26-12	2-16-15	6-19-13
Þ	LOCALITY WHERE CULTURES WERE MADE AND DATE	Priest River, Idaho (Experiment Station) 10-4-12*	Priest River, Idaho 10-6-12,* 'A	Missoula, Mont. 10-10-14*	Priest River, Idaho 10-6-12,* A	Priest River, Idaho 10–6–12*	Missoula, Mont. 12-22-14†	Priest River, Idaho (Experiment Station) 10-4-12,* A
	Locality	Ore.	Local	Mont.	Local	Local	Cal.	Idaho
SISOI	Source of seed	Cal.	Local	N.M.	Local	Local	Cal.	Minn.
TRIAL HOSTS	Name and number used in cultures	Pinus ponderosa (2)	Pinus ponderosa (2) Local	Pinus ponderosa (2) N.M.	Pinus contorta (2) Local	Pinus contorta (2) Local	Pinus Jeffreyi (2)	Pinus resinosa (2)

*Cultures in field. † Greenhouse. ‡ All color names taken from Ridgway's color standards and nomenclature.

ate: former floral spikes for floral spikes for floral spikes for floral	both pistil- live yellow gorous, light it pistillate, light drab; dark green- ve (no. 627).	s staminate, SZ			pronounced lants small, neter.	illate plants 52); parent	inate plants h olive (no. rk greenish
December 14, 1916: 3 infections, 2 on one stem 2 cm. apart, 1 staminate, 1 pistillate; former 4 cm. high, stems vinaceous drab, floral spikes wax yellow, mature (no. 623); latter 2.5 cm. high, light yellowish olive (no. 623); third infection plant, pistillate, 5 cm. high, not uniformly yellowish olive, internodes purplish gray, fruit not produced (no. 624); parent uniformly yellowish olive, 4 cm. high (no. 625).	December 14, 1916: 1 on each host, both pistillate, 1 stunted, 4 mm. high, olive yellow (no. 626); other 3.5 cm. high, vigorous, light yellowish olive (no. 626); parent pistillate, 6 cm. high, honey yellow, fruit light drab; staminate stems on same branch, dark greenish olive, floral spikes yellowish olive (no. 627).	October 14, 1916: 1 infection, plants staminate, 3 cm. high, greenish yellow, had flowered, parent staminate, plain yellow (no. 684).	May 1, 1916: Penetration of sinker; no further result.	May 1, 1916: Penetration of sinker; no further result	November 1, 1916: I infection; pronounced fusiform swelling of branch, plants small, barely protruding, 1 mm. in diameter.	October 14, 1916: I infection, pistillate plants 3 cm. high, honey yellow (no. 652); parent (no. 643).	October 13, 1916: 2 infections; staminate plants 4 cm. high, mature, dark greenish olive (no. 653); pistillate, 3 cm. high, dark greenish olive (no. 654); parent (no. 643).
		6-26-13	2-16-15	2-16-15	2-26-13	6-26-13	: : : :
Spokane, Wash.	Spokane, Wash.	Priest River, Idaho 10–6–12*	Missoula, Mont. 12-22-14†	Missoula, Mont. 10-14-14	Missoula, Mont. 10-21-14†	Priest River, Idaho 10-6-12*	Spokane, Wash. $^{11-10-11,*}B$
Spokane	Spokane	Idaho	Mont.	Idaho	Idaho	Local	Cal.
Europe	Europe	Idaho	Mont.	Europe	Europe	Local	Ore.
Pinus sylvestris (2) Europe	Pinus montana (2)	Larix occidentalis (4)	Larix occidentalis (4) Mont.	Larix europea (4)	Picea excelsea (1)	Abies grandis (2) Local	Abies concolor (2)

by the parent when growing on what we may term the mother host, the limitations of a species are naturally more difficult to define. Notwithstanding this change, however, a good species should be sufficiently characteristic on any host and under any of the ordinary conditions of growth as to be readily recognized by one having a wide knowledge of the plant in the field. We do not think of the low, scrubby Douglas fir of central Montana as anything different from the gigantic form of this tree occurring in the Puget Sound region.

It is of considerable economic importance that *R. campylopoda* will infect *Pinus resinosa*, *P. sylvestris*, and *P. montana*, and may be expected to be a serious pest on these trees in localities where conditions are favorable. In drier sites of the Lake states and, in fact, throughout the Northeast, where it is proposed to plant *P. resinosa*, this mistletoe would undoubtedly grow luxuriantly. and care should be exercised against its introduction into these regions on nursery stock during the early period of infection.

Seeds of R. campylopoda were sown on the following pines in most cases in the greenhouse, but either due to the poor quality of the seed, loss of seed, or low vigor of the trial hosts the results were mostly negative. This does not mean, however, that all of the species mentioned here are immune. In a few cases infection did occur on species not mentioned in the table, but the results were of a nature that it is thought best not to report them at this time. These were Pinus Banksiana, P. mayriana, P. Strobus, P. Cembra, P. cembroides, P. edulis, P. Lambertiana, and P. monticola. Sowings made on Pseudotsuga taxifolia, Larix leptolepis, Tsuga heterophylla, Thuja plicata, T. occidentalis, Cupressus arizonica, Picea Engelmanni, P. canadensis, Populus tremuloides, P. trichocarpa, Betula occidentalis, Alnus tenuifolia, Acer glabrum, and Prunus demissa resulted negatively.

SUMMARY.—Results of cultures so far indicate that the mistletoes known under the names *Razoumofskya campylopoda* and *R. cryptopoda* are distinct. Each form, however, may exhibit considerable variation, due to geographic location and host. The relationship of the two forms will be further considered when a number of experiments now being conducted are completed. Cultures show that the plant known as R. occidentalis abietina on Abies is in all probability a biological form of R. campylopoda.

The taxonomic position of the plant, however, cannot be established with any certainty until it is successfully grown on yellow pine.

Cultures with larch mistletoe

From the fact that this parasite, R. laricis Piper (figs. 9, 10), exhibits considerable variation under different conditions of growth and will occasionally grow on other hosts than Larix, it seemed desirable to study the species in culture. The chief results of these experiments



Fig. 9.—R. laricis on Larix occidentalis: staminate and pistillate plants.

are embodied in table II. These results indicate that Larix is the true host genus for R. laricis. The fact that 6 trees of Larix

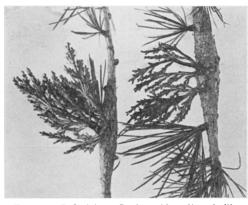


FIG. 10.—R. laricis on Larix occidentalis: pistillate plants; reduced one-half.

occidentalis were infected out of 6 on which seed were sown demonstrated the close affinity of the host and parasite. The readiness with which R. laricis infects Larix europea and L. leptolepis, the common Japanese larch, shows that this parasite may be expected to cause serious injury to plan-

tations of these species not only in America, but in many parts of Europe and Japan as well, wherever climatic conditions are

TABLE II

Seed collected at St. Maries, Idaho, September 24, 1911; Priest River, Idaho, September 20 and 30, 1912; from R. laricis on Larix occidentalis; ALL CULTURES MADE IN THE FIELD.

TRIAL HOSTS	OSTS		T COLLEGE		RESULTS OF CULTURES
Name and number used in cultures	Source of seed	Locality grown	DE	Date of first observation of germination	Results (measurements averaged)
Larix occidentalis (2) Local	Local	Local	Coeur d'Alene, Idaho 11-5-11		Coeur d'Alene, Idaho 11-5-11 August 25, 1915: 2 infections; plants staminate, 2.5 cm. high; flowers reed yellow, 3 and 4- parted, stems olive yellow; parent lime green, upper half of fruit purplish lilac.
Larix occidentalis (2)	Local	Local	Blue Lake, Idaho 10-3-12	6-18-13	October 14, 1916: 2 infections on one host; plants pistillate, 4 cm. high, stems dark livid purple; spikes olive yellow developed in direct light; parent uniformly light yellowish olive, grew in diffused light.
Larix occidentalis (2) Local	Local	Local	Missoula, Mont. 10-30-12	6-6-13	September 8, 1915; 2 infections, pistillate, 4.5 cm. high, stems olive ocher, fruit lime green, culture in dense shade; parent dark olive buff, fruit with pale bluish lavender points, growing in strong light.
Larix europea (2)	Europe	Wash.	Spokane, Wash. 11-11-11		October 13, 1916: 3 infections, I staminate, 2 pistillate; former 3 cm. high, dark vinaceous brown, mature in 1914, flowers lime green, flowers mostly 3-parted (no. 658); latter 2 cm. high, joints dark vinaceous brown, fruit dark greenish olive (nos. 656 and 657); parent; pistillate stems dark livid brown, fruit light yellowish olive (no. 659); staminate stems on same branch, olive yellow flowers, mostly 4-parted (no. 685).

Larix leptolepis (2) Japan	Japan	Idaho	Priest River, Idaho 10-4-12	6-19-13	6-19-13 October 15, 1916: I infection, pistillate, 2 cm. high, stems light yellowish olive, fruit with bluish tips (no. 654); parent dark livid purple (no. 655)
Pinus ponderosa (6) Local	Local	Local	Coeur d'Alene, Idaho		August 25, 1915: I infection, plants pistillate, 4 cm. high, dark greenish olive, vigorous at time of collection (no. 662); parent honey yellow (no. 663).
Pinus contorta (6) Local	Local	Local	Blue Lake, Idaho 10–6–12	6-18-13	6-18-13 October 14, 1916: 1 infection, staminate, 3 cm. high, stems yellowish olive, joints dark vinaceous drab, flowers distantly alternate-opposite, mostly 3-parted (no. 660); parent; pistillate, stems dark vinaceous brown, fruit light yellowish olive (no. 661); staminate, stems on same host anthracene purple, flowers mostly 4-parted, closely alternate-opposite.
Abies grandis (6) Local	Local	Local	Blue Lake, Idaho 10–2–12	6-18-13	6-18-13 October 14, 1916: 1 infection; staminate, apparently vigorous for a time, but at this date plants were dead and mostly fallen; original color not determined with certainty but appeared purplish (no. 664); parents light yellowish olive with darker colored fruit (no. 665).

favorable. The nature of the results on *Pinus ponderosa* and *P*. contorta, although demonstrating that this mistletoe under very favorable conditions will infect yellow pines, does not show any great affinity for the genus. When it is recalled that 900 seeds were sown on 18 individuals of *Pinus ponderosa*, each receiving 50 seeds, resulting in one infection, and one infection on P. contorta out of 12 trees tested with 600 seeds, the relationship between these 2 tree species and the larch mistletoe cannot be very close. The same is apparently true with regard to the infection of Abies grandis. trees were tested with the usual number of seeds, but only I infection resulted, which later died. These cultures also show that seeds germinating in the most vulnerable places only cause infection. Out of 500 seeds sown on Larix only 10 were able to cause infection, although apparently all the seeds which remained on the trees germinated. All were sown on parts of branches or shoots not over 6 years old, and care was taken to place the seeds favorably. It is to be expected that some of the seeds in outdoor cultures are removed by wind, rain, snow, insects, or birds. The observations relative to the favorableness of seed placement do not apply in the same way to the cultures on Pinus and Abies, since the larch mistletoe does not exhibit any marked affinity for these genera. That the same species of mistletoe growing on different hosts or under different conditions on the same host may exhibit different morphological characters is clearly demonstrated by these cultures.

Since these experiments with the larch mistletoe were started, the following field observations have been made near Fernan Lake, Idaho. A large veteran western larch severely infected with *R. laricis* was left standing in a clearing which reseeded to *Pinus ponderosa* and *P. contorta*. From one each of these species growing directly under the larch typical, although small, specimens of the larch mistletoe bearing both pistillate and staminate plants were collected. The only true pine mistletoe in the immediate vicinity was *R. americana*. In a canyon near Missoula, Montana, where the larch is seriously infected with *R. laricis* and the pine mistletoes are not known to occur, specimens of the former have been collected from a single infection on *Pinus contorta*. These results are very

much at variance with previous ideas of the host affinities of R. laricis, but they should not alter in the least the economic situation, since infections very rarely occur. The fact that both pines and larches are resinous may explain the occasional occurrence of the parasite on the former hosts. Although great pains were taken to place the seed in favorable places on the trial hosts, the results on the following species were negative: Pseudotsuga taxifolia, Pinus monticola, Picea Engelmanni, Thuja plicata, Tsuga heterophylla, Taxus brevifolia, Juniperus communis, Populus tremuloides, P. trichocarpa, Betula occidentalis, Alnus tenuifolia, and Salix Bebbiana. Field observations on the intermingling of the branches of most of these species with severely infected branches of larch-bearing pistillate plants confirm the results of the cultures. Such observations, however, cannot be used as conclusive evidence for determining the host range for any one species of mistletoe.

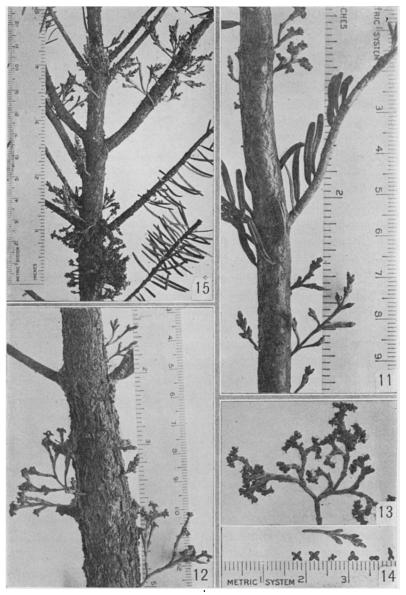
Summary.—The hosts of Razoumofskya laricis are Larix occidentalis, L. Lyalli, L. europea, L. leptolepis, Abies grandis, Pinus ponderosa, and P. contorta. The parasite is known to be of economic importance to the first named species only. The plant resulting from an infection on any other host than that on which it normally grows exhibits considerable change in morphology and also in vigor. That different degrees of exposure with respect to light very greatly influence the color of the plants is very clearly demonstrated.

Cultures with Razoumofskya species having purple flowers

A group of small mistletoes found in the western United States has one character in common with *R. pusilla* of the East, namely, deep purple flowers.⁶ They are *R. Douglasii abietina* (Engelm.) Piper⁷ on *Abies* (figs. 11, 12), *R. Douglasii* (Engelm.) Kuntze on *Pseudotsuga* (fig. 15), and a small form on *Picea* (figs. 13, 14). A careful comparison of representative collections of these 3 plants from varied environments shows no constant characters by which they may be held as distinct species. All three have 2, 3, or rarely

⁶ Weir, J. R., Wallrothiella Arceuthobii. Jour. Agric. Research 4:372. 1915.

⁷ Reported by ENGELMANN under the name Arceuthobium Douglasii var. abietinum in S. Watson, Bot. Cal. 2:106. 1880.



FIGS. 11-15.—Fig. 11, R. Douglasii on Abies grandis, staminate and pistillate plants; fig. 12, R. Douglasii on Abies lasiocarpa, staminate and pistillate plants; fig. 13, small purple-flowered form on Picea Engelmanni, staminate plant, natural size; fig. 14, small purple-flowered form on Picea Engelmanni, staminate flowers and pistillate plant; fig. 15, R. Douglasii on Pseudotsuga taxifolia, staminate and pistillate plants.

4-parted purple flowers, solitary or clustered, simple or branched, according to age of infection, bloom and fruit in the same season; and size of fruit, flower, plant, and color of stems show some variations under different conditions of growth. Cross inoculations involving these forms should demonstrate whether or not all 3 are identical with *R. Douglasii*. The results of a series of cultures are given in tables III and IV.

At the time these cultures with R. Douglasii and R. Douglasii abietina were made seeds of the form on Picea were not available. The plant is not morphologically different from the other two, and cultures now under way indicate that it will infect Abies and Pseudotsuga. The evidence so far obtained is so pointedly in favor of the view that all 3 forms are identical that there can be little room for doubt. We find, for instance, that R. Douglasii will infect Abies grandis, A. lasiocarpa, and A. concolor, which are hosts for R. Douglasii abietina. No marked morphological differences are found in the resultant plants and their parents, any more than is to be expected from a change of host or condition of growth. The same is true for the culture of this mistletoe on Picea Engel-The evidence that all 3 forms are identical is further strengthened by the fact that R. Douglasii abietina from Abies lasiocarpa will infect Pseudotsuga taxifolia and Abies grandis, and that it is possible to fertilize the pistillate flowers of this form on the latter host with pollen from plants on Pseudotsuga. These results demonstrate the relationship of the 3 small purple-flowered forms here considered. The two forms on Abies and Picea should be considered identical with R. Douglasii in view of the foregoing results. It has already been pointed out that, in the writer's experience, the plants on Abies and Picea are in most cases found in localities where R. Douglasii abounds. If the former were specifically distinct, with inherent tendencies to select their particular hosts, they should in the light of our knowledge of the well defined species be more abundant. On the contrary, they are never found in any quantity. The conclusion that R. Douglasii does not abundantly infect other trees than Douglas fir is also shown by the following observations. The writer has looked several times in vain for infection of this species on Abies and Picea when the

Seed collected October 28, 1911, September 20, 1912, and October 1, 1914, at Missoula, Montana, from R. Douglasii on Pseudolsuga taxifolia.

TABLE III

TRIAL HOSTS	OSTS				RESULTS OF CULTURES
Name and number used in cultures	Source of seed	Locality	LOCALITY WHERE TESTS WERE MADE AND DATE	Date of first observation of germination	Results (measurements averaged)
Pseudotsuga taxifolia (2)			Priest River, Idaho 10-5-12*	6-17-13	April 14, 1916: I infection; staminate, I.5 cm. high, solitary, dark olive gray, flowers blackish purple; parent, light yellowish olive with lighter colored flowers; former in direct light, latter in shade.
Abies lasiocarpa (2)	Mont.	Mont.	Missoula, Mont. 10-24-14†	2-8-15	Pronounced swelling at several points; apparent infections; plants never appeared.
Abies grandis (2)	Mont.	Mont.	Missoula, Mont. 10-24-14†	2-6-15	One infection but died out; host in poor condition.
Abies grandis (2)			Priest River, Idaho 10–5–12*	6-17-13	October 14, 1916: I infection; pistillate, plants 2 cm. high, simple, solitary, light yellowish olive, fruit dark greenish olive, mature, flowers fertilized from plants resulting from inoculation on Pseudolsuga which were 2 m. distant, seed were immediately sown on Pseudolsuga; parent brownish, 3 cm. high, were deep olive gray with slightly lighter colored fruit.
Abics concolor (2)			Spokane, Wash. 11-10-11*		April 14, 1916: I infection, staminate, 2 cm. high, solitary, shender, light yellowish olive, flowers vernonia purple, 2 and 3-parted, in shade (no. 670); parent, 3 cm. high, clustered, branched, yellowish olive, with purplish fruit, grew in direct light; staminate, 2.5 cm. high, clustered, branched, rather thick for species, olive bulf, flowers vernonia purple, 3-parted, grew in shade.
Picea Engelmanni (2)			Priest River, Idaho 10-5-12*	6-17-13	April 14, 1916: 1 infection; staminate, 2.5 cm. high, solitary, branched, flowers vernonia purple, plants light yellowish olive (no. 676); parent, pistillate, 3 cm. high, simple, solitary, dark olive gray with purplish tipped fruits (no. 677); staminate, 3 cm. high, clustered, simple, flowers dark corinthian purple.
* Cultures in field.	Greenhouse.				

TABLE 1V

SEED COLLECTED ON BALD MOUNTAIN NEAR LAKE PEND OREILLE OCTOBER 2, 1912, FROM R. Douglasii abiclina on Abies lasiocarpa.

RESULTS OF CULTURES	Results (measurements averaged)	April 14, 1916: 1 infection; staminate, 2 cm. high, solitary, branched, light yellowish olive, flowers blackish purple (no. 678); parent (no. 679), not differing in any particular feature with the exception of staminate flowers of parent plants were slightly larger and of a lighter color.	6-18-13 April 14, 1916: 1 apparent infection, swelling of branch; plant did not appear.	6-17-13 October 14, 1916: 1 infection; pistillate, solitary, branched, 3 cm. high, light yellowish olive, fruit mature, artificial pollination from no. 678, brownish purple at tips, seed immediately sown on <i>Pseudolsuga</i> ; parent, 3.5 cm. high, simple, solitary, dark olive-gray, fruit dark greenish olive (no. 681).
	Date of first observation of germination	6-17-13	6-18-13	6-17-13
	LOCALITY AND DATE	Priest River, Idaho 10-6-12	Blue Lake, Idaho 10-9-12	Priest River, Idaho 10-8-12
	Locality	Local	Local	Local
0STS	Source of seed	Local	Local	Local
TRIAL HOSTS	Name and number used in cultures	Pseudotsuga taxifolia (4) Local	Pseudotsuga taxifolia (4) Local	Abies grandis (4) Local

latter grew in absolute contact with brooms on Douglas fir bearing pistillate plants. As previously stated, however, this is not conclusive evidence of the host range of a species. Accident of infection is too great; besides, trees growing in such juxtaposition are very often suppressed, thus reducing the amount of vulnerable tissue. These results were obtained only by the most careful placing of the seeds at the most susceptible points. In the course of years such conditions occur in nature. Afterward, as a matter of course, further infection from the parent tree to others of its kind may be easier. The type of broom produced by *R. Douglasii* varies with age and host. On hosts with strongly excurrent growth, such as *Abies lasiocarpa* and *A. grandis*, the brooms are usually erect, but drooping or swaying forms occur. The erect type of broom is common on *Pseudotsuga taxifolia* during the first years of infection, but later may assume the weeping willow form.

Seeds from plants on Abies lasiocarpa were sown on a single individual each of Tsuga heterophylla, Larix occidentalis, Pinus monticola, Thuja. plicata, and Populus trichocarpa, but without results. Seeds from plants on Pseudotsuga taxifolia were without result on these hosts and also on Larix europea, Picea sitchensis, P. canadensis, P. excelsea, P. Parryana, Sequoia gigantea, Pinus ponderosa, P. contorta, P. Jeffreyi, P. sylvestris, Betula occidentalis, Alnus tenuifolia, and Pyrus. The several species of Picea were not in a vigorous condition, having been transplanted only a short time before the seed were sown.

Summary.—The foregoing cultures indicate that Razoumofskya Douglasii abietina is identical with R. Douglasii. The hosts of R. Douglasii as known to the writer are Pseudotsuga taxifolia, Picea Engelmanni, Abies concolor, A. grandis, A. lasiocarpa, A. nobilis, and A. amabilis. The species is of economic importance only on Pseudotsuga taxifolia.

Cultures with lodgepole pine mistletoe

This species (R. americana [Nutt.] Kuntze) (figs. 16, 17) is one of the most characteristic of the genus. In order to determine its host range, the results of some recent cultures are presented in table V. It is shown that *Pinus contorta* is the true host of R.

americana, but that occasionally other hard pines are attacked. The writer has previously reported the occurrence of this mistletoe

on Pinus attenuata, P. Jeffreyi, and P. ponderosa, and it has long been known to be common on Pinus Banksiana in Canada. The fact that this mistletoe will infect Pinus montana, the common mountain pine of Europe, further supports the writer's contention that it may be expected to occur occasionally on any of the hard or yellow pines, and also is a warning that the parasite would probably find a favorable home in Europe. The plant apparently attacks the vellow pines other than Pinus contorta with difficulty.



Fig. 16.—R. americana on Pinus ponder-osa: staminate plants.

Such infections are by no means common, and frequently result in some morphological changes in the plant. These changes, how-



Fig. 17.—R. americana on Pinus contorta: pistillate plants.

will never be of consequence in this respect, is shown by the discovery of two infections on Pinus albicaulis near Darby,

ever, may not be any more marked than those the plant may exhibit when developing under various light intensities or varying conditions of nourishment on its regular host. If *R. americana* exhibits a certain antipathy to other yellow pines, it apparently has a much greater aversion to white pine. That the species will infect white pines but with difficulty, and his respect, is shown by the

TABLE V

Seed collected at Libby, Montana, October 18, 1911; Priest River, Idaho, October 1, 1912; and at Coeur D'Alene, Idaho, November 14,1914, from R. americana on Pinus contorta.

RESULTS OF CULTURES	first Results (measurements averaged)	6-18-13 April 13 and October 14, 1916: 1 infection on each tree, slight swelling of branch on stem, 2 staminate, 2 pistillate (no. 666), not varying in any marked degree from parent plants.	April 13, 1916: 2 infections at the same node on a single stem, only 1 tree infected, plants staminate and pistillate; former 4 cm. high, stems olive yellow; latter 5 cm. high, stems yellowish olive, fruit light dull glaucous blue (no. 667); parent; staminate, 8 cm. high, light yellowish olive with older parts of stem deep grape green; pistillate, 4 cm. high, uniformly dark olive gray, both stems and fruit (no. 668).	2-16-15 October 10, 1915: 1 infection, slight swelling, branch died, plants did not appear.	December 14, 1916: 1 infection; staminate, 5 mm. high, pronounced swelling of branch, excessive infiltration of resin, 2 small plants barely appeared in 1915, died out; another plant appeared just above original point of infection but remained small (no. 669).
	Date of first observation of germination	81-9	81-9	2-16	
	LOCALITY WHERE CULTURES WERE MADE AND DATE	Blue Lake, Idaho 10–2–12*	Blue Lake, Idaho 10-2-12*	Missoula, Mont.	Spokane, Wash. 11–10–11*
	Locality	Local	Local	Mont.	Spokane
STS	Source of seed	Local	Local	Mont.	Europe
TRIAL HOSTS	Name and number used in cultures	Pinus contorta (4) Local	Pinus ponderosa (4) Local	Pinus ponderosa (1)	form) (4)

* Cultures in field. † Greenhouse.

Montana. The parasite in this case caused unusually large and elongated swellings on the main stem of young trees, but the plants apparently were never able to come to maturity, remaining about 5-8 mm. high. One of the pines was transplanted into the greenhouse, and the context of the swelling shriveled up in a manner indicating that it was composed of very spongy tissues. The tree, however, remained living. The fact that 220 seeds of R. americana were sown on 6 different species of white pines with no result except the germination of the seeds further supports this observation. The trees tested were Pinus Lambertiana, P. monticola, P. Strobus, P. edulis, P. cembroides, and P. Cembra. R. americana is reported by COULTER and NELSON⁸ on Pinus flexilis. results of sowings on Larix europea, L. occidentalis, Picea sitchensis, P. Engelmanni, P. excelsea, Abies nobilis, A. lasiocarpa, A. grandis, Tsuga heterophylla, Pseudotsuga taxifolia, Thuja plicata, Taxus brevifolia, Populus trichocarpa, Betula occidentalis, and Alnus tenuifolia were negative.

Summary.—The hosts of Razoumofskya americana are Pinus contorta, P. Banksiana, P. attenuata, P. Jeffreyi, P. montana, P. ponderosa, P. flexilis, and with difficulty P. albicaulis. The plant is of economic importance so far as known only on the two first named species. Morphological changes are induced by change of host or condition of growth, but not to an extent that this, the most characteristic of all members of the genus on pines, could be confused.

Cultures with hemlock mistletoe

In the St. Joe National Forest, Idaho, are several areas of almost pure stands of *Tsuga heterophylla* heavily infected with *R. tsugensis* (figs. 18, 19). In the border zones of these areas a form of mistletoe has been collected on *Abies grandis* and *A. lasiocarpa* which varies in a number of details from the form collected on the same hosts in regions where the large mistletoe on *Pinus ponderosa* occurs. In order to see whether this is a case of *R. tsugensis* infecting other hosts than the common western hemlock, and also to determine its host range in general, the cultures given in table VI were made.

⁸ New Manual of Botany of the Rocky Mountains. 146. 1909.

R. tsugensis is not confined to species of Tsuga as heretofore believed, but will infect Abies lasiocarpa. The mistletoe most closely resembling R. tsugensis in point of color and size is the form R. occidentalis abietina, but as the results from cultures stand at present there is apparently no relation between them. The foregoing results indicate that the plant occasionally found on firs in the same vicinity with R. tsugensis is the common hemlock mistletoe,

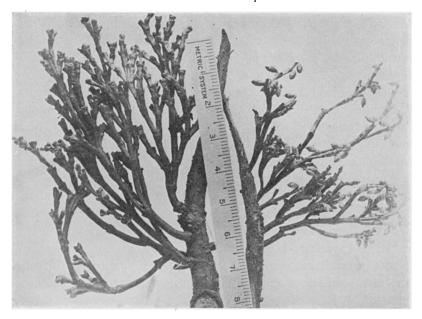


Fig. 18.—R. tsugensis on Tsuga heterophylla: staminate and pistillate plants; large form.

and also that this species may be expected to occur occasionally on other hosts than hemlock. Cultures may be considered fully completed when the plants found on Abies in the vicinity of R. tsugensis, also the form on Abies which has been referred to the yellow pine mistletoe, are shown by culture to infect Tsuga and Pinus respectively.

SUMMARY.—Seeds were also sown on Abies grandis, Pinus ponderosa, Picea orientalis, Larix occidentalis, and Pseudotsuga taxifolia, but the results were negative. The hosts of Razoumofskya

tsugensis are Tsuga heterophylla, Tsuga canadensis, and Abies lasiocarpa. So far as the present cultures show, the hemlock mistletoe will not infect Pinus, Picea, Larix, and Pseudotsuga. The fact that this mistletoe will infect Tsuga canadensis indicates the possibility of it becoming a pest in the native regions of other species of hemlock and is a condition to be guarded against.

Conclusion

Cultures at present indicate that R. campylopoda and R. cryptopoda are not identical. Each form may exhibit considerable varia-

tion, due to geographic location and host. It is shown that R. campylopoda will infect Pinus resinosa, and care must be taken to prevent it from getting a foothold in the eastern United States. It will also infect Pinus sylvestris and P. montana, and should be prevented from entering Europe or plantations of these trees in America. It is also indi-

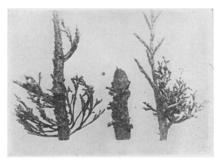


Fig. 19.—R. tsugensis on Tsuga mertensiana: staminate (center) and pistillate plants; small form; reduced one-half.

cated that the plant known as R. occidentalis abietina is a biological form of R. campylopoda.

R. laricis will infect Larix europea, L. leptolepis, Abies grandis, Pinus ponderosa, and P. contorta. All are new hosts for this species except the last. The parasite apparently readily infects the Japanese and European larch and would be expected to cause serious damage to these trees. Abies grandis, Pinus contorta, and P. ponderosa are infected with difficulty. This parasite so far as known at present is of economic importance only on Larix occidentalis.

The mistletoe known under the name R. Douglasii abietina is shown to be identical with R. Douglasii and should be written under the latter name. R. Douglasii is only of importance on Pseudotsuga taxifolia.

TABLE VI

Seed collected at Missoula, Montana, January 22, 1915, adhering to brooms and mistletoe plants on Tsuga heterophylla sent FROM ASHFORD, WASHINGTON, AND FROM THE SAME HOST IN ST. JOE NATIONAL FOREST, IDAHO, SEPTEMBER 30, 1914

TRIAL HOSTS	OSTS				RESULTS OF CULTURES
Name and number used in cultures	Source of Locality seed grown	Locality grown	LOCALITY WHERE CULTURES WERE MADE AND DATE	Date of first observation of germination	Results (measurements averaged)
Abies lasiocarpa (1)	Mont.	Mont.	Missoula, Mont. 1–28–15†	2-29-16	2-29-16 January 3, 1917: 1 infection, staminate, 2 cm. high, leaf green (no. 686); parent, 6 cm. high, light yellowish olive.
Tsuga canadensis (1)	Wis.	Wis.	Spokane, Wash. 10-7-13*	5-1-15	October 12, 1916: 1 infection, staminate, very slight swelling, 4 cm. high, dark greenish olive (no. 682); parent light brownish olive (no. 683).

*Cultures in field. † Greenhouse.

R. americana will infect both hard and soft pines, the latter with difficulty, and is of importance only on Pinus contorta and P. Banksiana of the former group. This mistletoe will infect Pinus montana and may be of consequence if introduced into Europe.

R. tsugensis will infect Abies lasiocarpa, thus possibly explaining the position of certain rare plants occasionally found on Abies in the vicinity of the hemlock mistletoe. This parasite will infect Tsuga canadensis and would probably cause serious damage to this tree in the East.

Cultures show very clearly that many of the characters employed in the classification of the false mistletoes vary with change of host, geographical location, and with various other environmental factors. This indicates that only the broader and plainly evident lines of demarcation should be employed in their classification.

Office of Investigation in Forest Pathology Bureau of Plant Industry Missoula, Mont.